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# On the RIP: using Relative Impact Potential to assess the ecological impacts of invasive alien species

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## Abstract

Invasive alien species continue to arrive in new locations with no abatement in rate, and thus greater predictive powers surrounding their ecological impacts are required. In particular, we need improved means of quantifying the ecological impacts of new invasive species under different contexts. Here, we develop a suite of metrics based upon the novel Relative Impact Potential (RIP) metric, combining the functional

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response (consumer *per capita* effect), with proxies for the numerical response (consumer population response), providing quantification of invasive species ecological impact. These metrics are comparative in relation to the eco-evolutionary baseline of trophically analogous natives, as well as other invasive species and across multiple populations. Crucially, the metrics also reveal how impacts of invasive species change under abiotic and biotic contexts. While studies focused solely on functional responses have been successful in predictive invasion ecology, RIP retains these advantages while adding vital other predictive elements, principally consumer abundance. RIP can also be combined with propagule pressure to quantify overall invasion risk. By highlighting functional response and numerical response proxies, we outline a user-friendly method for assessing the impacts of invaders of all trophic levels and taxonomic groups. We apply the metric to impact assessment in the face of climate change by taking account of both changing predator consumption rates and prey reproduction rates. We proceed to outline the application of RIP to assess biotic resistance against incoming invasive species, the effect of evolution on invasive species impacts, application to interspecific competition, changing spatio-temporal patterns of invasion, and how RIP can inform biological control. We propose that RIP provides scientists and practitioners with a user-friendly, customisable and, crucially, powerful technique to inform invasive species policy and management.

**Keywords**

biological control, ecological impacts, functional response, invasive alien species, numerical response, propagule pressure, relative impact potential metric, risk assessment

## Introduction

In recent decades, the tourism, agriculture, aquaculture, horticulture and pet trades, among others, have been boosted by new globalised transport networks (Hulme 2009, Seebens et al. 2018), facilitating novel pathways for invasive alien species (IAS; herein invasive species) to spread and establish (Zieritz et al. 2016, Seebens et al. 2019). Indeed, the number of confirmed invasive species per country has risen around 70% since 1970 (IPBES 2019). The combination of species introductions with changing climate (Seebens et al. 2015, Gallardo et al. 2018) and other anthropogenic impacts (MacDougall and Turkington 2005, Didham et al. 2007) is aiding species establishment and spread, with the number of invasive species unlikely to saturate in the near future (Seebens et al. 2017). While the effects of invasive species can be benign (invasiveness is not correlated with impact: Ricciardi and Cohen 2007), many invasive species have severe ecological consequences that drive negative economic, social and health implications (Laverty et al. 2015a,b). Assessing and predicting such ecological impacts are crucial to prevent and mitigate invasions (Simberloff et al. 2013). Note that here, we define ecological impact as changes in populations of affected species, principally through consumption of living resources by animals (e.g. predator-prey) and interspecific competition for limited resources (especially in plants - see Dick et al. 2017a,b,c and "Understanding and predicting competition with RIP" section below). Further, predicting which future species are likely to exert ecological impacts, and how such impacts are likely to change under different abiotic and biotic contexts, are vital objectives for the conservation of biodiversity worldwide (Dick et al. 2017a, IPBES 2019).

The management of invasive species is challenging, with certain high-profile failed management programmes (Bergstrom et al. 2009, but see Simberloff 2009). Successful

prediction of impact is vital to successful prevention, which is deemed the most effective invasive species management (Piria et al. 2017) and one that may avoid unpredictable indirect effects, such as trophic cascades (Jackson et al. 2017). Aichi Biodiversity Targets of the Convention on Biological Diversity focus on invasive species prevention, requiring a list of priority invasive species and preventative measures by 2020. EU legislation (Regulation No 1143/2014), alongside the list of IAS of Union Concern (Regulation No 2016/1141), and subsequent updates (Regulation Nos 2017/1263, 2019/1262), add further impetus to impact prediction, requiring all member states to develop evidence-based lists of invasive species likely to impact biodiversity and ecosystem services.

Here, we develop a suite of metrics based on the *per capita* effects and abundances of species (Dick et al. 2017c) that can quantify the spectrum of benign through to severely damaging invasive species. We outline the background to these metrics, the development of their key components, namely *per capita* effects (principally the functional response), the consumer population response (i.e. the numerical response), incorporation of risk (i.e. propagule pressure) and suitable proxies for these three elements. We then demonstrate the versatility of the metrics across abiotic and biotic contexts, including the prediction of climate change effects on invasive species impacts, how native species and established invaders can offer biotic resistance, how evolution can affect impact, aspects of interspecific competition, spatio-temporal patterns of invasion and impact, and the assessment of biological control agent efficacy.

## Background and development of invasive species ecological impact metrics

Numerous studies have failed to find traits of species, spanning diverse taxonomic and trophic groups, that reliably predict invader ecological impact (Hayes and Barry 2008, Ricciardi et al. 2013, Dick et al. 2014; but see Valdovinos et al. 2018, Fournier et al. 2019 for recent studies on specific taxa). While some have found traits that predict invasiveness (Hui et al. 2016), there is no correlation between invasiveness (i.e. establishment and spread) and ecological impact (Ricciardi and Cohen 2007). Parker et al. (1999) proposed the impact (I) of an invader as the product of its range (R), abundance (A) and its *per capita* effect (E):

$$I = R \times A \times E \quad (1)$$

Following this "Parker-Lonsdale" equation, Dick et al. (2013, 2014) proposed the classic metric of the functional response (see Fig. 1) could be used as a universal *per capita* effect in invasion ecology. Functional responses typically describe the rate of prey capture by a predator in relation to prey density (Solomon 1949, Holling 1959), however, they can be applied to any consumer/resource interaction (see Dick et al. 2017a,b,c), including herbivores (Farnsworth and Illius, 1996), microbial communities (Graves et al. 2016) and nutrient uptake rates by plants (Tilman 1977,

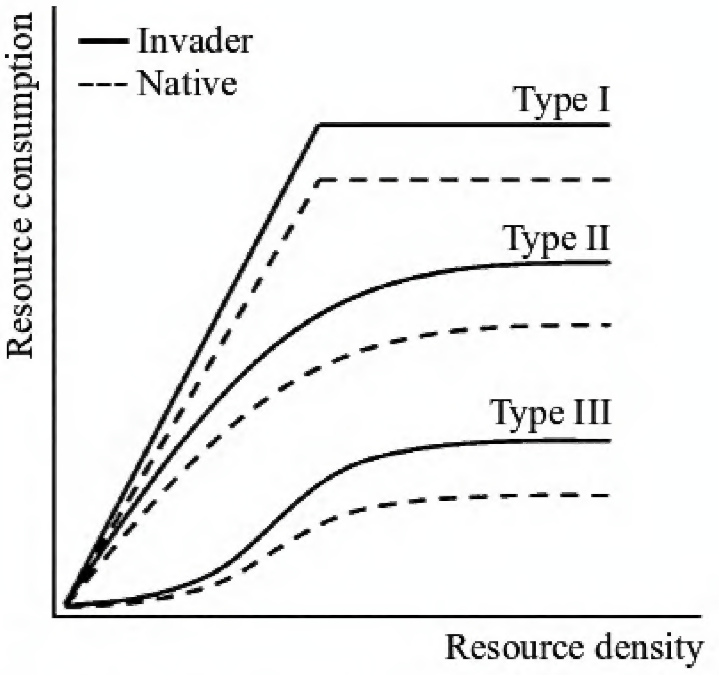


**Figure 1.** Type I, II and III functional responses and hypothetical invader/native comparisons (see Dick et al. 2014).

Rossiter-Rachor 2009). Indeed, the concept of functional responses in plants was the basis of the "functional resource-utilisation responses" proposed by Tilman (1977). By focusing on resource sequestration rate, functional responses quantify the strength of primary ecological interactions exhibited by any species, and hence can potentially unify invasion ecology across trophic and taxonomic groups (Dick et al. 2017a,b). Indeed, resource acquisition is at the core of the majority of longstanding hypotheses in invasion ecology (Catford et al. 2009, Ricciardi et al. 2013).

Comparing the functional responses of native and invader consumers can highlight differences in the strength of consumer/resource interactions (Fig. 1), with implications for population stability of the prey or other resources (Holling 1959, Dick et al. 2014). Type I functional responses are typical of filter feeders (Jeschke et al. 2004) with a directly proportional increase in resource consumption with availability; Type II responses are hyperbolic and inversely density-dependent; and Type III responses are sigmoidal, with low consumption at low resource densities. Type II responses may have a destabilising effect due to high proportional resource consumption at low resource densities, while Type III responses may have a stabilising effect due to low proportional consumption at low resource densities (Dick et al. 2014). Type III may arise when consumers switch to more abundant resources (Van Leeuwen et al. 2007) or when habitat complexity offers refuge for prey (Alexander et al. 2012).

The comparative functional response approach (Fig. 1), whereby the impacts of invasive species are compared with analogous native species as eco-evolutionary baselines (Dick et al. 2017c), have proved a reliable tool for explaining the ecological effects of existing invasive species and predicting the impacts of new, emerging and indeed potential future invaders under a wealth of different contexts (Dick et al. 2014, 2017a, b, c, Crookes et al. 2018, Howard et al. 2018, Hoxha et al. 2018). Such contexts include dissolved oxygen levels (Laverty et al. 2015a), habitat complexity (Wasserman et al. 2016), temperature regimes (Zamani et al. 2006), water chemistry gradients (Kestrup

et al. 2011), higher order predators (Barrios-O'Neill et al. 2014) and parasites (Laverty et al. 2017b). Such studies are not limited to the laboratory either, with numerous examples of functional responses estimated from field studies (Goss-Custard et al. 2006, Smout et al. 2014). Further, Penk et al. (2017) illustrated the utility of this approach, providing a framework for its application across a range of novel organisms. Finally, the comparative functional response approach can be applied to asking which of several actual or potential invaders will have more or less impact, with several studies indicating that higher functional responses (i.e. maximum feeding rates) do indeed predict higher ecological impact. For example, the killer shrimp (*Dikerogammarus villosus*) has consistently higher maximum feeding rates than the less ecologically damaging demon shrimp (*Dikerogammarus haemobaphes*: Bovy et al., 2014), with a similar effect being noted for the invasive golden apple snail relative to other introduced snails (Xu et al. 2016). With regards to plants, it is notable that resource utilization curves, which are essentially functional responses, can be used comparatively to understand the dynamics of plant invasions (e.g. Rossiter-Rachor et al. 2009). Most recently, the utility of determining functional responses of multiple populations of the same invasive species was shown by Howard et al. (2018) and Boets et al. (2019), with functional responses derived within and between geographical populations tracking actual impacts in the field. Further, a recent study of multiple populations of the invasive crayfish *Faxonius limosus* shows context-dependencies of functional response parameters (Grimm et al. 2020), and the authors caution that risk assessments of invasive species should, where possible, be based on multiple population estimates of functional responses. This recognition of population level as opposed to species level differences is now a burgeoning question and we encourage more research in this area.

Although the comparative functional response approach has been successful in characterising ecologically damaging invasive species by itself (e.g. Dick et al. 2013, Alexander et al. 2014, Dick et al. 2014, 2017a,b,c), it may provide limited quantification of total ecological impact as the functional response is only one of the three components of the aforementioned Parker-Lonsdale equation (Eq. 1: Parker et al. 1999). Since "range" is dependent on time since invasion, and is not necessarily a species characteristic (Kumschick et al. 2013), the ecological impact of a species can be viewed as a function of its *per capita* effects and some measure of the number of individuals involved (Dick et al. 2017c, Pearse et al. 2019). The latter is often measured as the consumer population numerical response, but often more simply as consumer abundance (Dick et al. 2017c). Assessment of both functional response and numerical response (or proxies) is crucial. For example, Fig. 2 illustrates that high ecological impact will result when both the functional and numerical responses of an invader are high, but impact may also result when a few individuals demonstrate particularly high functional responses, or when the functional responses of invaders are similar to natives but invader numerical response is very high. Note also from Fig. 2 that high invader numerical responses alone do not necessarily equate to high, or indeed any noticeable impact if there are low levels of inter-specific interactions, or no detectable interaction (see Dick et al. 2017c; Fig. 2). Indeed, this method proposes that relatively low functional and/or numerical responses can be used to identify low impact or relatively

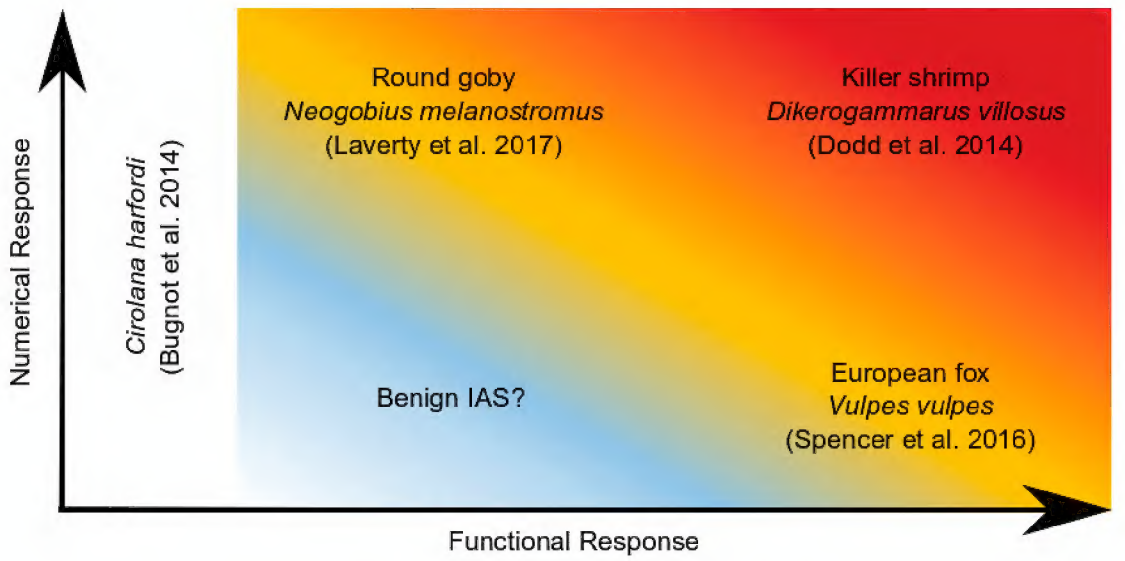


**Figure 2.** Ecological impact heat map of the combination of functional and numerical responses of invasive species compared to trophically analogous equivalents, with ecological impact increasing from bottom left to top right (see text for details).

benign invaders (Fig. 2). Here, we thus propose that Relative Impact Potential (RIP, see below), which incorporates functional responses and numerical responses into a ratio for invader and native analogues, offers a way to identify the range of impacts of invasive species illustrated in Fig. 2.

## The Relative Impact Potential metric for quantification of invasive species ecological impacts

The combination of functional and numerical responses is consistent with the idea of the total response (TR) of a consumer (Holling 1959):

$$TR = FR \times NR \quad (2)$$

Unlike the functional response, the rather nebulous numerical response has proven difficult to derive due, for example, to time lags in consumer population responses (see Dick et al. 2017c, Laverty et al. 2017a), resulting in the need for more simplistic and pragmatic proxies for the numerical response that capture consumer reproduction, aggregation and resource assimilation (Dick et al. 2017c). Consequently, Dick et al. (2017c) proposed that the "Impact Potential" (IP) of an invader can be represented as the product of the functional response (FR) and a chosen proxy for the numerical response ($NR_{proxy}$), such as field abundance/density (AB: see Dick et al. 2017c, Laverty et al. 2017a), giving an equation that blends Eq.1 and Eq. 2:

$$IP = FR \times NR_{proxy} \quad (3)$$

e.g.

$$IP = FR \times AB \quad (4)$$

An IP value by itself offers limited insight, but we relate the IP of an invasive species to the IP of a trophically analogous native (the baseline, or co-evolved relationship), giving the "Relative Impact Potential" of the invader (henceforth, RIP) as:

$$\text{RIP} = \left( \frac{\text{FR invader}}{\text{FR native}} \right) \times \left( \frac{\text{NRproxy of invader}}{\text{NRproxy of native}} \right) \tag{5}$$

In Eq. 5, the functional response may be the maximum feeding rate, that is, the curve asymptote, or $1/h$ (where $h$ is the handling time parameter: Dick et al. 2017c), or, where this is not possible, the consumer feeding rate with an over-abundance of resource supply. However, the latter will lack the benefits of the functional response method, which gives the extrapolated maximum feeding rate ($1/h$) and resolution of potentially destabilising Type II versus stabilising Type III functional responses (see Fig. 1). When the resulting RIP value is < 1, this predicts the invader will have less impact than the trophically analogous native; when RIP = 1, we predict invader impact no different from that of the native; and when RIP is > 1, we predict the invader will have a greater impact than the native (Dick et al. 2017c). The native comparator thus allows the degree of ecological impact of the invader to emerge, and RIP values do indeed correlate positively with actual ecological impacts of invasive species in the field (Dick et al. 2017c, Laverty et al. 2017a, Kemp et al. 2018). The choice of native comparator(s) can be guided by assessment of those native species that are trophically similar to the invader and found in the invader's new range, with multiple native comparators useful if available (see Dick et al. 2017c). For example, comparing invasive *Dikerogammarus villosus* with both *Gammarus pulex* and *G. duebeni celticus* gives coverage of almost all of the UK/Ireland and many European mainland freshwaters (Bollache et al. 2008), and Rossiter-Rachor et al. (2009) successfully compared the invasive gamba grass with two locally abundant and analogous native grasses.

RIP lends itself to data collection by experiment and/or survey, or information from already available/published results. Single estimates of the functional response and the numerical response proxy may be used in the RIP equation; alternatively, means, standard errors, variances, standard deviations or confidence intervals can allow the incorporation of uncertainty into RIP. To do this, it is assumed that the observed functional response and numerical response proxy are samples from underlying distributions of values (see Dick et al. 2017c). With both measures being positive, a log-normal form for both underlying distributions is used, giving the probability density function (pdf) for the RIP measure given the four input pdfs (two numerators, two denominators):

$$f(\text{RIP}) = \left( \frac{f(\text{ FR invader })}{f(\text{ FR native })} \right) \times \left( \frac{f(\text{ NRproxy of invader })}{f(\text{ NR proxy of native })} \right) \tag{6}$$

where $f()$ = the pdf.

As an example, we have functional responses for the Ponto-Caspian invasive amphipod *D. villosus* (killer shrimp) and the native analogue *G. duebeni* towards *Asellus*

*aquaticus* prey (Bollache et al. 2008). Abundances were taken from Berezina & Duris (2008) and Dick (1996) respectively, giving RIP as:

$$\text{RIP}=\left(\frac{\text{FR } D.villosus}{\text{FR } G.duebeni}\right)\times\left(\frac{\text{AB } D.villosus}{\text{AB } G.duebeni}\right)=\left(\frac{22}{16}\right)\times\left(\frac{230.5}{31.6}\right)=10.03$$

We can then use the pdf, $f$(RIP), and report RIP and the confidence intervals (80% and 60%) and the probability that RIP is greater than 1, or any other figure (e.g. >10; see Dick et al. 2017c). By using the means and SDs from the worked example above [i.e. mean (SD) = 22(3.5), 230.5(23.3), 16(1.7), 31.6(5.4)], we get:

$$f(\text{RIP})=\left(\frac{f(\text{FR } D.villosus)}{f(\text{FR } G.duebeni)}\right)\times\left(\frac{f(\text{AB } D.villosus)}{f(\text{AB } G.duebeni)}\right)$$

$$\text{RIP}=10.44\begin{pmatrix}80\%CI=4.36-51.8\\60\%CI=7.98-12.7\\P\text{RIP}>1=100\%\\P\text{RIP}>10=50.8\%\end{pmatrix}$$

The result can also be visualised using "RIP biplots", with maximum feeding rate on the x-axis, and the numerical response proxy on the y-axis (e.g. Laverty et al. 2017b; Cuthbert et al. 2018b, c). Using an example from Laverty et al. (2017a; Fig. 3), scanning diagonally from the origin to the top right of the plot, the invasive top mouth gudgeon *Pseudorasbora parva* has a greater ecological impact than the native bitterling *Rhodeus amarus*. Here, the numerical response proxy is fish field abundance but alternatives may be available (see below).

The other classic functional response parameter "*a*", the attack rate, is an alternative to the maximum feeding rate. This quantifies the initial gradient of the functional response curve, and gives insights into the critical impact a consumer exerts at low resource densities (Dick et al. 2014). Cuthbert et al. (2018c) show the consistency of the maximum feeding rate and attack rate as functional response measures for two copepod species, *Macrocyclops albidus* and *Megacyclops viridis*, at three different temperatures. However, Dickey et al. (2018) reveal a noticeable difference between these two metrics for two turtle species, with *Trachemys scripta troostii* demonstrating a high maximum feeding rate but a low attack rate, and *Kinosternon subrubrum* demonstrating the reverse. However, a solution to the dilemma of whether to use *a* or *h* has emerged, with the unified metric of FRR, the Functional Response Ratio, which is simply *a*/*h* (Cuthbert et al. 2019).

There may be difficulties in determining functional and numerical responses, for example, practicalities surrounding consumer and resource supply, or ethical issues. Hence, we now review proxies for both.

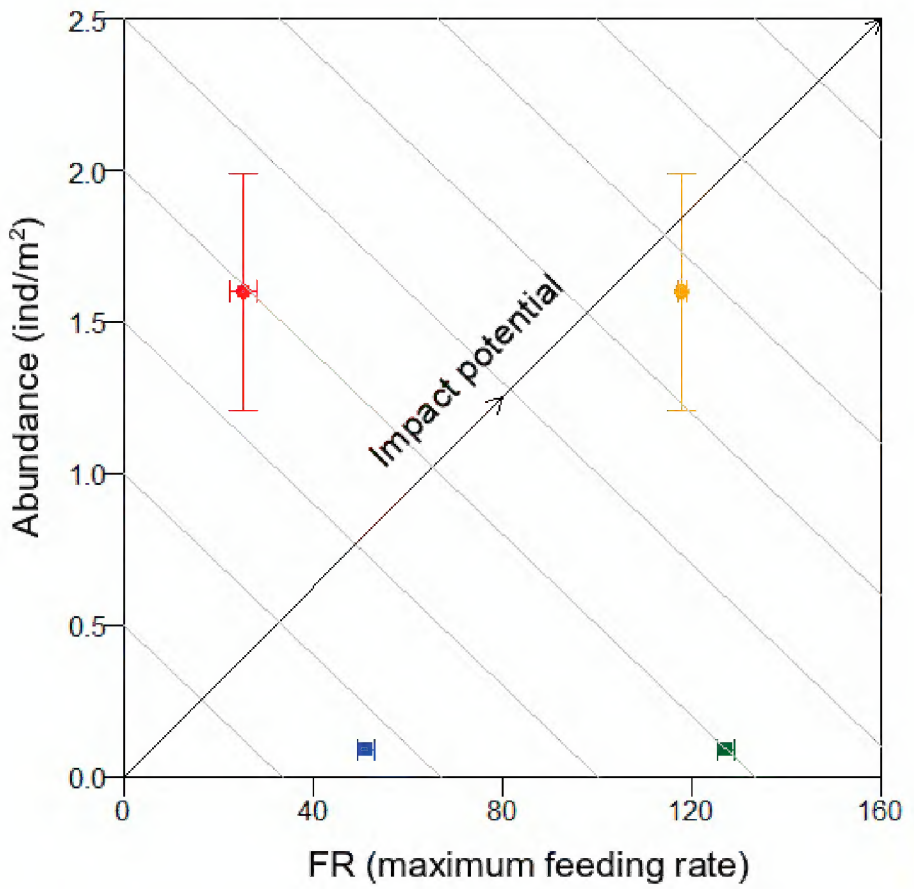


**Figure 3.** RIP biplot from Laverty et al. (2017a): invasive top mouth gudgeon *Pseudorasbora parva* (red and orange circles representing prey type 1 and 2 respectively), has a greater ecological impact than the native bitterling *Rhodeus amarus* (blue, prey type 1, and green, prey type 2, squares).

## Choosing appropriate functional response proxies

In some situations (e.g. large-bodied species in the wild) functional response experiments may prove difficult. For example, the functional responses of deer species are poorly described (but see Illius et al. 2002), but there are proxies in the literature, such as absolute daily intake rate (e.g. Newman et al. 1998). Intake per metabolic body mass ($kg^{0.75}$) is a proxy (Drożdż 1979) that allows comparison of trophic analogues differing in body size (e.g. Reeves' muntjac, *Muntiacus reevesi*, versus native British deer species). For plants (e.g. Rossiter-Rachor et al. 2009), there are a number of metrics from resource uptake curves that are analogous to functional response metrics, such as $V_{max}$ (maximum uptake rate over time) and $K_m$ (substrate concentration at 50% maximum uptake rate).

As per Dick et al. (2017c), offering an over-abundance of a resource in experiments could suffice as a functional response proxy, however, highly informative aspects such as curve type will not then be available (see Fig. 1) and such an over-abundance may lead to unrealistically high consumption rates. On the other hand, low consumption rates can emerge from gregarious prey defence behaviours (e.g. the postulated Type IV functional response: Jeschke and Tollrian 2000). Consequently, where possible, we strongly recommend performing full functional response experiments/surveys, with a range of resource availability, to maximise information.

## Choosing appropriate numerical response proxies

Population abundance/density are backed theoretically and in practice as suitable proxies for the numerical response (Dick et al. 2017c, Laverty et al. 2017a). These can be derived in numerous ways, such as through monitoring programmes, and from estimates of consumer densities from non-native ranges. In most cases, relative abundance is a sufficient proxy, with the effort required to determine absolute abundance often better spent on extra sampling (Hayes et al. 2007). One example of a fisheries technique directly proportional to abundance is Catch Per Unit Effort (CPUE; Maunder and Langley 2004), and there are numerous other techniques for estimating abundance and density for both open and closed populations (e.g. Seber 1986, Hayes et al. 2007; Suppl. material 1: Table S1).

Where abundance/density data are not suitable, for example, due to large body size differences among species, biomass is a suitable proxy. For example, the invasive sharptooth catfish *Clarias gariepinus* reaches lengths of 148 cm (Clay 1984), whereas the native trophic analogue river goby, *Glossogobius callidus*, reaches only 12 cm (Greenwood 1994, Alexander et al. 2014). The benefit of using biomass instead of abundance for this example is demonstrated in Fig. 4, which gives a more realistic demonstration of impact for *C. gariepinus*. Further, for plant numerical response proxies, estimates of individuals per unit area proved useful in calculating RIP values for invasive gamba grass in comparison to native grass species (Dick et al. 2017c), and other measures such as biomass and percentage coverage could be utilised.

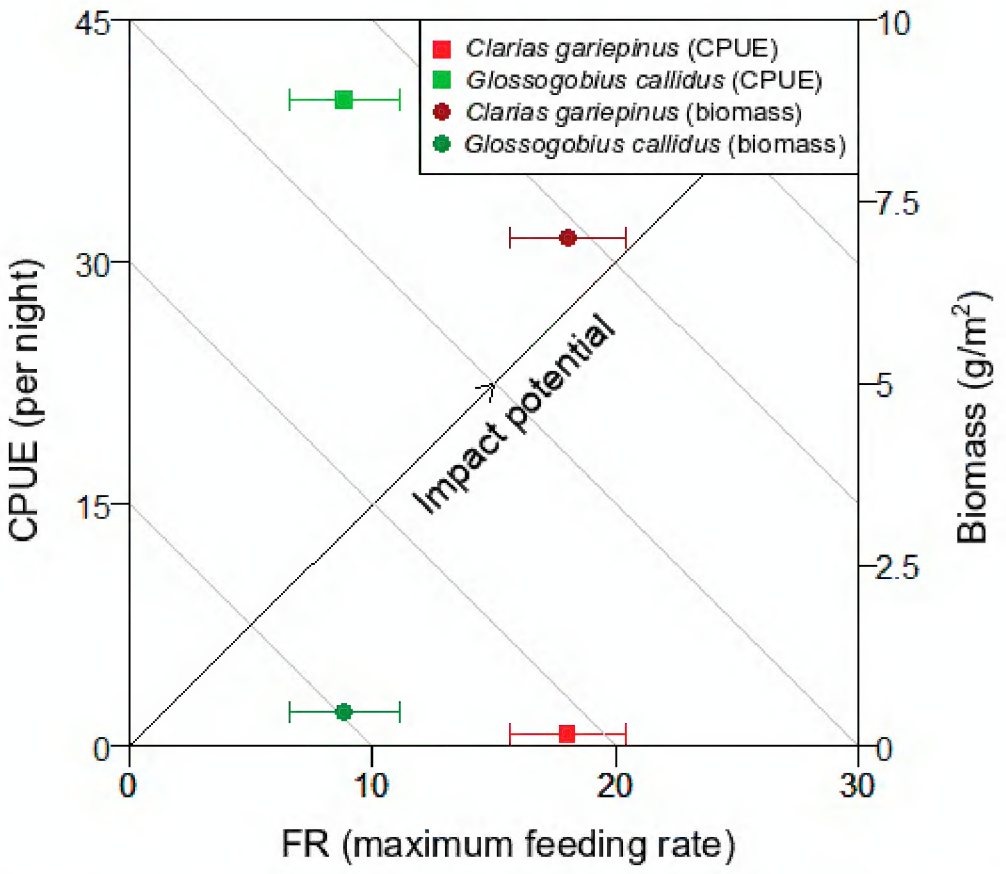


**Figure 4.** Comparison of impact derived from use of Catch Per Unit Effort and biomass, whereby CPUE gives a misleading impact assessment of the extralimital predator. CPUE data were taken from Bokhutlo et al. (2016) and Richardson et al. (2006), with unpublished biomass data from O.L.F Weyl taken from Dick et al. (2017c).

Often there is no known invasion history of a species, which will become increasingly common as new source pools of invaders are linked to human transport (Seebens et al. 2018). In such contexts, basing the RIP upon the abundance/density of the species in its native range, where it has co-evolved with natural enemies, could be misleading and it may be more prudent to use numerical response proxies based on other life history traits. For example, fecundity can be a key determinant of invasive species establishment (Grevstad 1999) and persistence (Pöckl 2007). While many highly fecund species never become invaders, and a large number of invaders have low fecundity, fecundity can strongly affect population size (Parvulescu et al. 2015). Thus, fecundity may be a pragmatic proxy for the numerical response (see Cuthbert et al. 2018b, Dickey et al. 2018). For example, in the abundance and fecundity impact biplot for two *Gammarus* species (Fig. 5), the invader *G. pulex* is compared with native *G. duebeni celticus*. We size-matched the two species by using the average size of the native (10–11mm: Hynes 1954), and took the corresponding mean number of eggs for the invader at that size (Hynes 1955). Abundance figures are from Kelly et al. (2006). The resulting biplots are consistent (Fig. 5), with *G. pulex* showing greater impact across both proxies of the numerical response, in line with actual field impacts. We outline further numerical response proxies in Suppl. material 1: Table S1.

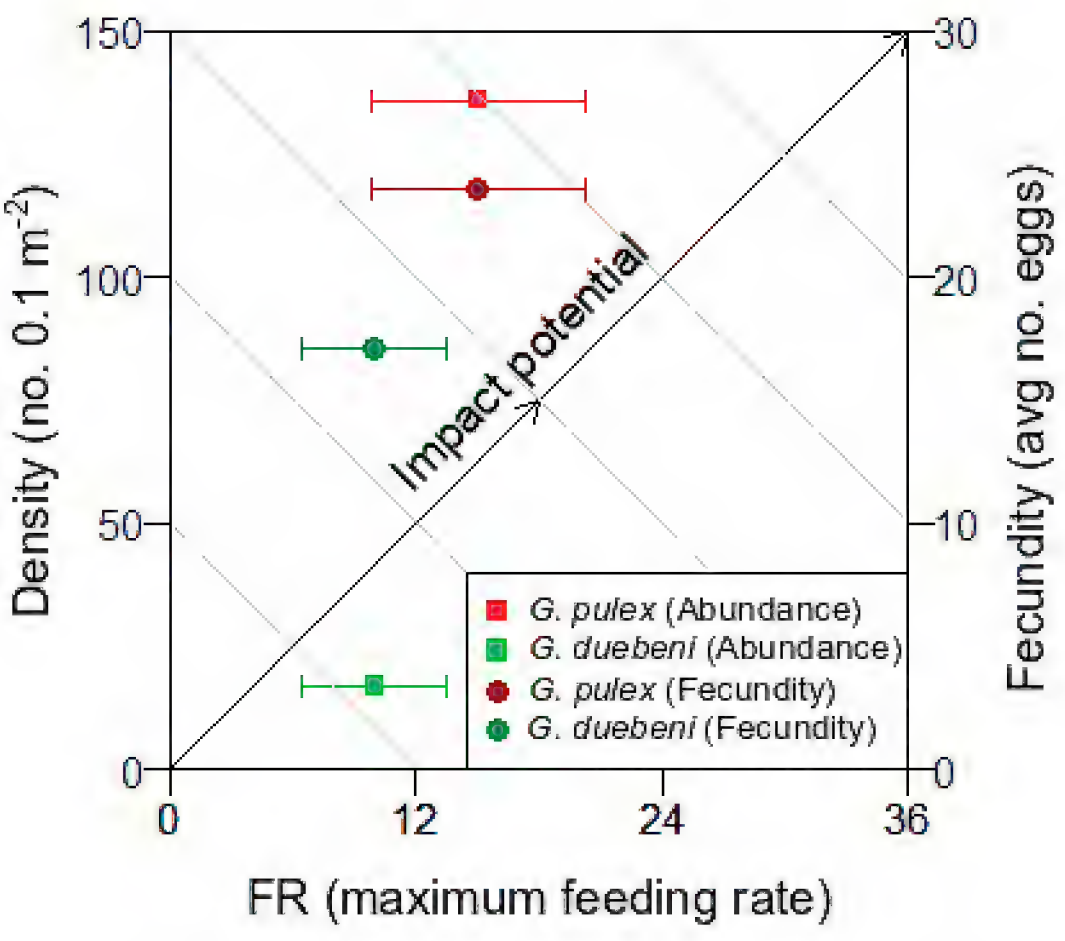


**Figure 5.** Comparing abundance and fecundity as numerical response proxies for the invader amphipod *G. pulex* and native *G. duebeni*. Functional response data taken from Laverty et al. (2015a), abundance taken from Kelly et al. (2006), and fecundity data taken from Hynes (1955).

## Incorporating risk into RIP: propagule pressure proxies and Relative Invasion Risk, RIR

Invasive species success can be heavily dependent on propagule pressure, that is, the number, frequency and viability of individuals introduced (Briski et al. 2012). Management prioritisation thus needs to balance the likely ecological impacts of an invasive species with its risk of arriving, establishing and spreading. Dickey et al. (2018), using terrapins in the pet trade, combined the RIP metric with the multiplier "Pet Propagule Pressure" (PPP) to calculate Invasion Risk (IR: Eq. 7):

$$IR = FR \times NR \times PPP \quad (7)$$

PPP took two forms: one assessed availability of the species across 20 pet stores; the other surveyed classified advertisement websites for unwanted pets. Three dimensional triplots (i.e. x-, y- and z-axes) visualise relative invasion risk i.e. RIR (R script available therein). Dickey et al. (2018) also proposed other proxies for propagule pressure, such as live wildlife import and export data (US Law Enforcement Management Information System), and studies assessing survivability in ship ballast water (Gollasch et al. 2000). Surveys that account for the role of horticulture in plant invasions (e.g. Bayón and Vilà 2019) and some invertebrate invasions (Cannon et al. 1999) could also offer valuable proxies of propagule pressure. We therefore propose that combining such proxies of propagule pressure alongside functional and numerical responses offers an effective three-pronged assessment and prioritisation method that assesses overall invasion risk.

## RIP in predicting invasive species impacts due to climate change

The past four years have been the hottest on record (2015–2018: NOAA 2019), and such changing environmental conditions will affect the establishment and impact of invading species (Kelley 2014, Iacarella et al. 2015a, Laverty et al. 2017b). Resultant changes in species range, phenology and physiology (see Bellard et al. 2012) may thus influence both functional and numerical responses. For example, temperature often influences functional responses (Englund et al. 2011) in a number of ways, affecting metabolism (especially for ectotherms: Gillooly 2001) and digestion efficiency (Pavasovic et al. 2004). Numerical responses will also be affected with, for example, many reptile species exhibiting temperature dependent sex determination (Laloe et al. 2014). Phenological shifts can also influence food availability and hence growth and abundance (Visser and Both 2005), potentially increasing the impact disparity between native and invader (Lediuk et al. 2014).

We thus propose that, for any invader, the effect of temperature increases (or other abiotic variables) on its ecological impact can be assessed by Eq. 8 as:

$$RIP = \left( \frac{\text{FR of invader at high temp}}{\text{FR of invader at low temp}} \right) \times \left( \frac{\text{AB of invader at high temp}}{\text{AB of invader at low temp}} \right) \quad (8)$$

where 'high temp' could be the mean environmental temperature projected from climate models. Note that abiotic variables such as temperature may not affect functional response and numerical response proxies linearly (e.g. feeding parameters can show hump-shaped responses to temperature: Englund et al. 2011), and this RIP formula compares snapshots of impact at the study temperatures of choice.

The rate of reproduction of the prey (or other resource e.g. plant growth and reproduction) will also likely be affected by the same temperature rise, thus either decreasing or increasing impact. For example, if reproduction by the prey increases at higher temperatures (e.g. Sutcliffe and Carrick 1981), then impact will be reduced. Alternatively, a prey species already close to its thermal tolerance may be stressed by temperature rise and thus actually reduce its reproductive allocation (Dhillon and Sharma 2009), increasing impact. We thus propose a modifier to Eq. 8 that we call the "Resource Reproductive Qualifier" (RRQ), defined as the reciprocal of the fraction or proportion to which reproduction changes with temperature (or other variable: Eq. 9):

$$\mathrm{RRQ} = 1 / \left( \frac{\text{Reproductive output of prey at the higher temperature}}{\text{Reproductive output of prey at the lower temperature}} \right) \tag{9}$$

For example, if a prey species doubles its reproductive output at the higher temperature, then this will halve the RIP value as it is multiplied by ½; alternatively, a prey species that halves its reproductive output at a higher temperature will double the RIP value (i.e. multiply RIP by 1/0.5=2). Eq. 8 thus becomes:

$$\mathrm{RIP\,q} = \left( \frac{\text{FR of invader at high temp}}{\text{FR of invader at low temp}} \right) \times \left( \frac{\text{AB of invader at high temp}}{\text{AB of invader at low temp}} \right) \times \mathrm{RRQ} \tag{10}$$

For example, South et al. (in prep) demonstrate that lionfish *Pterois volitans* exert higher predation upon shrimp *Palaemonetes varians* at 26 °C (max. feeding rate of 8.34 ± 0.65 SE) than at 22 °C (4.34 ± 0.55 SE) and that lionfish have greater abundances at the higher temperature (28.80 ± 1.75 SD $ha^{-1}$: Kulbicki et al. 2012 vs 21.20 ± 5.1 SD $ha^{-1}$: Whitfield et al. 2007), thus:

$$\mathrm{RIP} = \left( \frac{8.34}{4.34} \right) \times \left( \frac{28.8}{21.2} \right) = 2.611$$

However, their prey is likely to increase in abundance by 5% between the two temperatures, meaning RRQ is:

$$\mathrm{RRQ} = 1 / \left( \frac{1.05}{1} \right) = 0.952$$

Since more prey means the impact exerted lessens, this leads to a reduced RIP of:

$$\mathrm{RIPq} = 2.611 \times 0.952 = 2.486$$

However, we can see that the increased prey abundance due to temperature increase does not offset the increased feeding rate and abundance of the predator, leading to maintenance of an RIP value > 1.

RIP can thus be adapted with RRQ to include context dependencies like temperature, but also associated climate change conditions such as ocean acidification (Uthicke et al. 2013) and freshening (Casties et al. 2015), providing new predictive metrics for the vast array of climate change consequences for invasive species impacts.

## RIP as a measure of biotic resistance

Functional and numerical responses of resident species towards invasive species may provide biotic resistance (see also Twardochleb et al. 2012, Cuthbert et al. 2018c). For example, high functional responses of native and naturalised *Gammarus* species towards invasive prey *Crangonyx pseudogracilis* explain the field patterns of presence/absence of the invader (MacNeil et al. 2013, Cuthbert et al. 2018c). Using RIP, we propose here a powerful biotic resistance metric that can: (1) determine which native/naturalised species exhibit greater biotic resistance; and (2) predict the influence of abiotic factors on the strength of such biotic resistance (br). Thus, to assess which of two resident species better resists an invader:

$$\mathrm{RIPbr} = \left(\frac{\mathrm{FR\ of\ native1}}{\mathrm{FR\ of\ native2}}\right) \times \left(\frac{\mathrm{AB\ of\ native1}}{\mathrm{AB\ of\ native2}}\right) \quad (11)$$

Taking the functional response data of MacNeil et al. (2013) with non-native *C. pseudogracilis* prey, and the *Gammarus* spp. abundance data of Kelly et al. (2006), the RIPbr for the naturalised *G. pulex* relative to the native *G. duebeni* is:

$$\mathrm{RIPbr} = \left(\frac{\mathrm{FR}\ \textit{G. pulex}}{\mathrm{FR}\ \textit{G. duebeni}}\right) \times \left(\frac{\mathrm{AB}\ \textit{G. pulex}}{\mathrm{AB}\ \textit{G. duebeni}}\right) = \left(\frac{11.7}{9.1}\right) \times \left(\frac{136}{17}\right) = 10.29$$

Therefore, resistance to the non-native *C. pseudogracilis* prey by the naturalised *G. pulex* is stronger than by native *G. duebeni* due to higher *per capita* feeding rate and abundance.

One possible issue of using functional response data to infer biotic resistance is the use of a single prey species, unlikely in the wild where alternative prey will occur. We thus suggest functional response experiments feature the target invasive prey and additional native prey, coupled with experiments that explore the other classic ecological concept of prey "switching" or "frequency dependent predation" (Murdoch 1969). Prey switching, or lack thereof, has strong implications for the stability of prey populations and the biotic resistance that predators can exert upon invasive species. For example, Cuthbert et al. (2018c) assessed predation by the native amphipod *G. duebeni celticus* upon native mayfly larvae *Baetis rhodani* and invasive *C. pseudogracilis*. They noted similar Type II destabilising functional responses upon both prey species when offered separately. However, when both prey species were offered simultaneously, the predator

did not exhibit prey switching, and instead consumed disproportionately less of the invader, indicating a lack of biotic resistance. This matches field patterns, where the invader successfully colonises diverse communities, counter to the idea that high community diversity leads to high biotic resistance (Howeth 2017, Cuthbert et al. 2018c).

## RIP and the effect of evolution on invasive species impact

There is a notable lack of evolutionary theory for invasive species (Colautti and Lau 2015), but RIP could determine the drivers and consequences of adaptive evolution and thus help long-term decision-making. Siemann and Rogers (2001) highlighted that invasive species in receiving environments may be different from those in native ranges. In addition, Shine (2012) highlighted that differences in traits of a species can be evident when comparing the invasion front and long-colonised areas. Alleles coding for enhanced dispersal, aggression and rapid resource consumption are likely to accumulate within the invasion front, while alleles coding for slower dispersal will be confined in the long-colonised areas (Phillips et al. 2006, Shine 2012). Thus the dispersal process and selection may lead to differences in behaviour that increase impact on native species at invasion fronts (the Invasion Front Hypothesis: Iacarella et al. 2015b). In support of this hypothesis, front line *Hemimysis anomala* have higher attack rates (Iacarella et al. 2015b) and front line *Orconectes limosus* have greater clutch sizes (Parvulescu et al. 2015). Comparing front line and long-established populations with RIP could thus improve invasive species risk assessments by explicitly incorporating spatio-temporal variation in impact. We therefore propose:

$$\text{RIP} = \left( \frac{\text{FR of frontline pop.}}{\text{FR of long established pop.}} \right) \times \left( \frac{\text{AB of frontline pop.}}{\text{AB of long established pop.}} \right) \tag{12}$$

There are, however, a very limited number of studies of functional and numerical response changes with range expansion, and we can only encourage collection of data to populate Eq. 12 to test these ideas. We discuss other aspects of RIP in spatio-temporal contexts below.

Finally, the use of RIP in the evolutionary context could assist with a still relatively untested conservation technique, genetic backburning (Phillips et al. 2016). This involves moving long-established individuals ahead of the front line individuals, and slowing the progression of the invasion. RIP could test the ecological outcomes of such efforts.

## Understanding and predicting competition with RIP

Interspecific competition can reduce the abundances of interacting species and drive species exclusions and coexistence (Connell 1961, Tilman 1977, Schoener 1983, Oyugi et al. 2012). The patterns of resource use by, and the population densities of, inter-

acting species determine these outcomes. Hence RIP, by capturing both, could help to elucidate the role of competition in invasions. Tilman (1977) explicitly included the role of "functional resource-utilisation responses" in determining interspecific competition "winners" and "losers", a concept very close to the "functional response" as described by Holling and others. However, Tilman's examples were from plants and referred to competition over abiotic resources (e.g. Tilman 1977, 1982, 2004), while Holling and subsequent animal-focused researchers have viewed functional responses as determining impacts on living resources, especially prey (e.g. Holling 1959, 1966, Schoener 1974). While functional responses are implicit in competition theory (e.g. Abrams 1980), their routine measurement as determinants of interspecific competition outcomes is lacking in the literature, especially for animals. We contend this is due to what we call the "Competition Spectrum" (Fig. 6), whereby the role of differential use of shared and limiting resources in driving interspecific competition varies across trophic and taxonomic groups. In particular, plants compete for resources that are discrete, unique in the sense of not having equivalents (such as nitrogen), meaning that competing species cannot switch to analogous resources (Fig. 6). At the other extreme, a generalist predator has many potential prey items of some energetic and nutritional equivalence, and can switch between prey analogues, such that reduction of one prey item by a competitor (e.g. invader) could lead to little or no effect on interspecific competition (Fig. 6). Further, motility to find and utilise alternative resources increases from left to right in Fig. 6, thus decreasing the utility of functional responses in elucidating competition (i.e. potential competitors can reduce overlap in time and space). Along this spectrum lie, for example, filter feeders that can only utilise certain species/sizes of resource, with limited switching, and specialist predators that can at least move to new resource-rich areas and have some switching opportunities.

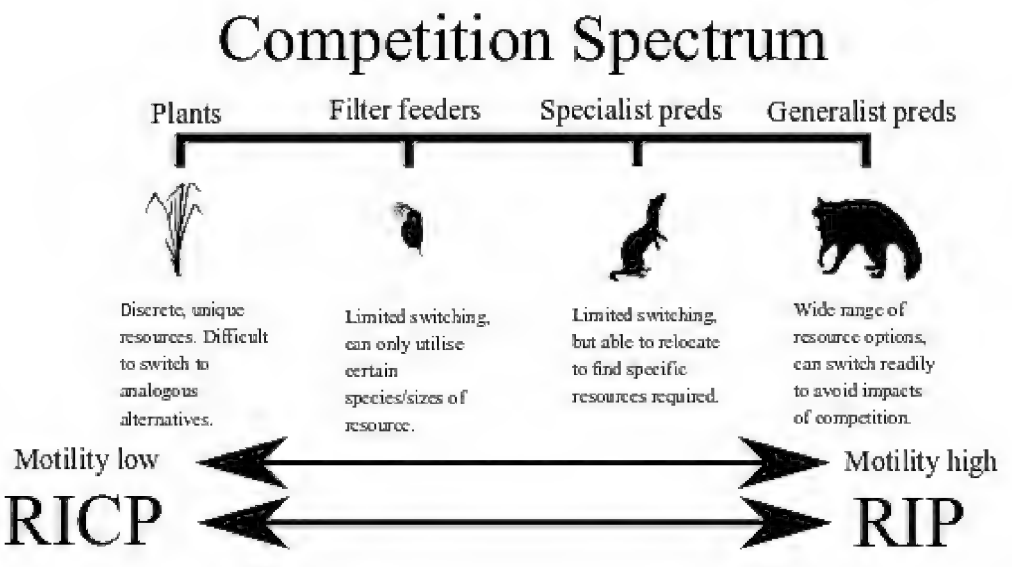
Competition Spectrum
Plants
Filter feeders
Specialist preds
Generalist preds
Discrete, unique resources. Difficult to switch to analogous alternatives.
Limited switching, can only utilise certain species/sizes of resource.
Limited switching, but able to relocate to find specific resources required.
Wide range of resource options, can switch readily to avoid impacts of competition.
Motility low
Motility high
RICP
RIP

**Figure 6.** The Competition Spectrum, outlining how differential use of shared and limiting resources drives interspecific competition, with outcomes varying across trophic and taxonomic groups. For example, plants compete for resources lacking equivalents, preventing competing species from switching to analogous resources, while generalist predators have many relatively equivalent potential prey items and the reduction of one prey item by an invader could lead to little or no effect on interspecific competition. We propose that RIP (Relative Impact Potential) will be most useful towards the right, whereas the same metric might better be named RICP (Relative Inter-specific Competitive Potential) to the left.

This spectrum perhaps explains why animal ecologists have simply not used functional responses in competition studies, while plant ecologists have done so for decades (see also Dick et al. 2017a). On the other hand, plant ecologists have not embraced the use of functional responses to explain and predict the identities of invader plants (but see resource use efficiency concept of Funk and Vitousek 2007); however, as pointed out by Dick (2017a, c), damaging invader plants may be identifiable from their higher maximum "feeding rates" (i.e. nutrient and other non-living resource uptake rates) compared to natives (e.g. Rossiter-Rachor et al. 2009). We propose that RIP as originally developed to assess impact on prey populations will be most useful towards the right of Fig. 6, whereas the same metric might better be named the Relative Inter-specific Competitive Potential to the left of Fig. 6. Thus, for example, we could assess the Relative Inter-specific Competitive Potential (RICP) as:

$$\text{RICP} = \left( \frac{\text{FRplant 1}}{\text{FRplant 2}} \right) \times \left( \frac{\text{ABplant 1}}{\text{ABplant 2}} \right) \tag{13}$$

For example, using the uptake rates of $NH_4^+$ of two grass species, the invasive *Andropogon gayanus* and the native *Eriachne triseta* (Rossiter-Rachor et al. 2009), and taking their respective abundance data from Parr (2010), we find the Relative Inter-specific Competitive Potential as:

$$\text{RICP} = \left( \frac{\text{FR } \textit{A. gayanus}}{\text{FR } \textit{E. triseta}} \right) \times \left( \frac{\text{AB } \textit{A. gayanus}}{\text{AB } \textit{E. triseta}} \right) = \left( \frac{11.6}{4.5} \right) \times \left( \frac{38.3}{5.1} \right) = 19.36$$

This large RICP value is congruent with the much greater general impact of the invasive species than the native analogue, particularly in terms of out-competing native plants.

Alternatively, it may be that the less commonly used functional response metric of attack rate offers greater insights into competition, since this captures the ability to effectively consume resources at low resource densities, reflective of Tilman's R* theory (Tilman 1982). Thus, calculating RIP with attack rates and abundances may better predict the degree of competition between species. We thus propose that Relative Inter-specific Competitive Potential could unify the plant-animal dichotomy in invasion science.

## Investigating spatio-temporal patterns of invasion using RIP

RIP as originally formulated assumed complete replacement of the native by the invader, for example, the invasion of *G. pulex* leading to the replacement of *G. duebeni celticus* by intraguild predation (Kelly et al. 2006). However, there are often lag phases between invasive species arriving and exerting impact (Coutts et al. 2018), with further

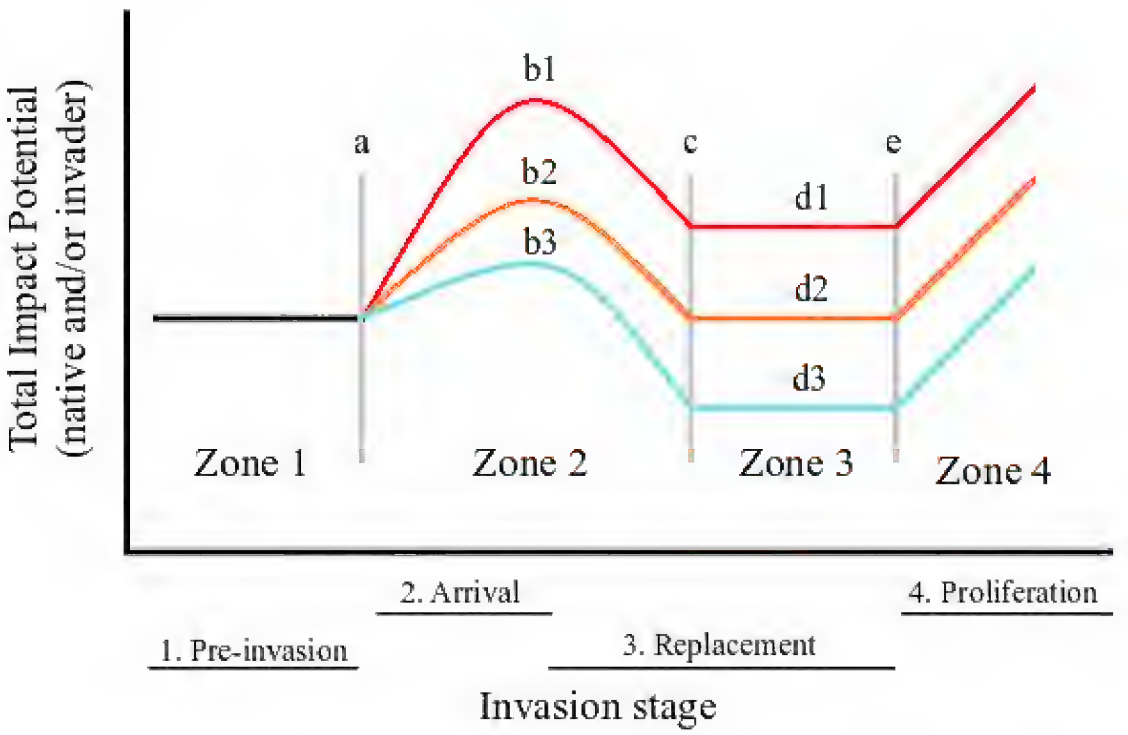


**Figure 7.** Conceptual spatio-temporal patterns of invasion impact across four invasion stages. In Zone 1, the "Pre-invasion" baseline impact is driven by the native species before the invader arrives, and at point "a" the invasion takes place. In Zone 2, additional impact is exerted by the "Arrival" of the invader, that is, impact is driven by invader and native combined, up to a temporary impact peak, which might vary in magnitude, denoted "b1–b3" in Zone 2. Following these peaks, impact declines as the invader replaces the native, with the point of complete "Replacement" denoted "c". In Zone 3, with only the invader now present, the impact level may remain higher than the native species baseline. Further, in Zone 4, after point "e", "Proliferation" of the invader may occur with consequent heightened impact. This scheme does not assume all stages will occur (e.g. partial replacement may persist) but outlines all likely scenarios.

time before total (or partial) species replacement. Hence, we outline four main zones in the fluctuation of invasive species impact potential over the course of an invasion (Fig. 7). In Zone 1 of Fig. 7, the "Pre-invasion" baseline impact is driven solely by the native species, and at point "a" the invasion takes place. In Zone 2, additional impact is exerted by the "Arrival" of the invader, up to a temporary impact peak, which might vary in magnitude, denoted "b1-b3" in Zone 2. Following these peaks, impact declines as the invader replaces the native, with the point of complete "Replacement" denoted "c". In Zone 3, with only the invader now present, the impact level may be higher ("d1"), or similar to ("d2"), or lower than ("d3") the native species baseline. Further, in Zone 4, after point "e", "Proliferation" of the invader may occur with consequent heightened impact. We can quantify the changes in total impact (Zone 2, 3 or 4) against the Zone 1 baseline, giving us Relative Total Impact Potential (RTIP). This is calculated by dividing the total impact potential of the invader and trophically analogous native species by the Pre-invasion baseline impact:

$$RTIP = \left( \frac{(FRnative \times ABnative) + (FRinvader \times ABinvader)}{(FRnative \times ABnative)} \right) \quad (14)$$

In a hypothetical example:
**Zone 2 (point b1, native + invader)**

$$\mathrm{RTIP} = \left( \frac{(10 \times 100) + (20 \times 200)}{(10 \times 100)} \right) = 5$$

An alternative scenario could result from one-sided intraguild predation, whereby the invader consumes the native and converts native abundance into its own. In this situation, the presence of the native species may lead to a greater abundance of invader than if the native had been extirpated:

$$\mathrm{RTIP} = \left( \frac{(10 \times 80) + (20 \times 250)}{(10 \times 100)} \right) = 5.8$$

Most studies fail to account for these potential changing impacts of an invader over time, and while there is a need to study the often acute initial effects of the invader, subsequent effects also need focus (Strayer et al. 2006).

## RIP application to biological control

Biocontrol agent selection targeting native or invader pests has commonly examined the functional responses of agents toward target organisms (Van Driesche and Bellows 2011, Cuthbert et al. 2018a,b). However, assessments of functional responses alone have frequently failed to forecast or explain biocontrol agent success in the field due to omission of context dependencies and a disregard for associated numerical responses of agents (Fernández-Arhex and Corley 2003). The application of RIP offers a holistic metric to assess and predict the comparative potential impact of biocontrol agents, denoted Relative Control Potential (Cuthbert et al. 2018b,d). The coupling of *per capita* effects (i.e. functional response) and proxies such as field abundance or fecundity estimates in the Relative Control Potential metric facilitates a rapid assessment of agent potential. Levels of uncertainty can also be projected using the pdf approach (see above), with biplots further enabling the clear illustration of comparative impact potential (Cuthbert et al 2018a,b,c). Moreover, Relative Control Potential can compare the impact of both native and non-native biocontrol agents under differing environmental contexts, reducing the potential for harmful effects commonly associated with 'classical' biocontrol agent releases (Simberloff and Stiling 1996). Non-native biocontrol agents are often unreliable and ecologically damaging (e.g. Azevedo-Santos et al. 2016), yet native analogues that exert similar impact levels may be available and should be preferentially selected. Relative Control Potential (Cuthbert et al. 2018b) is thus proposed as:

$$\mathrm{RCP} = \left( \frac{\text{FR of agent A}}{\text{FR of agent B}} \right) \times \left( \frac{\text{NR proxy of agent A}}{\text{NR proxy of agent B}} \right) \qquad (15)$$

Proxy selection for this metric can additionally be adjusted to suit the nature of biocontrol in respect to the method of release. Inoculative agent releases that seek to induce self-sustaining populations from a single introduction may be best to incorporate fecundity estimates, whilst temporary, inundative releases may be better suited to apply a proxy such as agent longevity. For example, Cuthbert et al. (2018b) compared the functional responses of two predatory cyclopoid copepods *Macrocyclops albidus* (agent A) and *Megacyclops viridis* (agent B) towards larvae of the West Nile virus vector mosquito *Culex pipiens*. Field abundance data for the two copepods originating from the same site (Tinson and Laybourn-Parry 1986) were integrated alongside attack rate ($a$) estimates from the functional responses, allowing comparison between the two species using RCP (Eq. 15):

$$\mathrm{RCP} = \left(\frac{1.98}{1.77}\right) \times \left(\frac{6727}{562}\right) = 13.39$$

Here, the Relative Control Potential value is substantially above 1, and thus *M. albidus* (agent A) is a much more efficacious agent of target mosquito prey than *M. viridis* (agent B). This corroborates with the demonstrated effectiveness of *M. albidus* in biocontrol applications aiming to reduce mosquito populations (Marten and Reid 2007).

To exemplify the influence of context dependency on biocontrol agent efficacy using Relative Control Potential, Cuthbert et al. (2018b) integrated functional response maximum feeding rates ($1/h$) of the same two copepods (*M. albidus*, agent A; *M. viridis*, agent B) across a temperature gradient (12–20 °C). Fecundity data for the two copepod species across matched temperatures from Laybourn-Parry et al. (1988) were then used to compare agents across temperatures:

$$\mathrm{RCP}_{12} = \left(\frac{15.88}{13.99}\right) \times \left(\frac{7.55}{8.28}\right) = 1.04$$

$$\mathrm{RCP}_{20} = \left(\frac{30.42}{33.25}\right) \times \left(\frac{12.66}{6.70}\right) = 1.73$$

Here, at 12 °C ($\mathrm{RCP}_{12}$), efficacies between agent A and agent B are relatively similar; however, as temperature increases to 20 °C ($\mathrm{RCP}_{20}$), differential efficacies in favour of agent A emerge. Thus, environmental context dependencies which alter the efficacy of biocontrol agents can be explicitly integrated into the Relative Control Potential metric.

## Future challenges

The Relative Impact Potential (RIP) metric addresses the lack of consistent quantification and representation of "ecological impact" in invasion ecology. Indeed, research has often focused on only one of the three components of the Parker-Lonsdale equation (Parker et al. 1999), and as a result ignored the "total response". What RIP offers is

a standardised, user-friendly means of quickly calculating the impacts of established invaders, potential invaders, relocated natives, and pests, relative to each other and trophically analogous equivalents. There is potential to account for a range of abiotic and biotic conditions over spatio-temporal scales, and to study the vast suite of mechanistic hypotheses within the invasion ecology literature. A challenge now is to ground-truth these metrics with real world examples, such as the positive relationship found between RIP and actual field impacts shown by Dick et al. (2017c).

We also recognise that RIP has to this point assumed linearity by assessing impact as the product of *per capita* effects and the numerical response (or proxy). We have hence assumed intraspecific interactions are neutral, rather than antagonistic or synergistic. We also note similarities with the "Density-Impact curve", which assesses non-linear effects of invasive species abundance with economic impact (Yokomizo et al. 2009). Currently, there are conflicting theories on whether antagonistic or synergistic interactions best facilitate invasion spread. For example, aggression towards conspecifics is thought to facilitate spread (e.g. aggressive individuals inhabiting the range frontier: Groen et al. 2012), while a lack of aggression towards conspecifics may facilitate coexistence in high densities in the invaded range (e.g. Argentine ant, *Linepithema humile*: Suarez et al. 1999). Calls for "bivariate FR approaches", i.e. functional response experiments with differing numbers of predators as well as prey, have thus been made (Médoc et al. 2013). We thus recognise that functional responses as derived from multiple predator experiments, revealing neutral, antagonistic or synergistic effects, must be conducted and such data incorporated into RIP metrics.

Until now, quantitative evaluations of impact have not been satisfactorily included in risk assessments (Blackburn et al. 2014, Dick et al. 2014). For example, Gallardo et al. (2016) required that scores be assigned based on the likelihood and magnitude of ecological impact. Uncertainty amongst assessors meant there were large standard deviations for invasive impact evaluation scores, suggesting a need for a more objective system. Blackburn et al. (2014) also encountered issues, presenting a risk assessment classification scheme heavily reliant on assessing the impact of invaders based on invasion history, which will be increasingly unavailable with new invasions. RIP offers a quantifiable measure of impact that avoids these pitfalls and removes the subjectivity inherent in horizon scans. By comparing non-native species to trophically analogous natives, the most potentially impactful invaders could be prioritised by RIP, and the addition of proxies for propagule pressure could highlight overall risk (Dickey et al. 2018). While certain impacts would not be covered by RIP, such as hybridisation, spread of disease and bio-fouling, expert opinion would still be required, allowing a rounded description of impact built upon quantitative foundations. RIP and its other derived metrics above thus require new data across a range of taxonomic and trophic groups, necessitating new and imaginative data collection methods (see also Dick et al. 2014). By providing a user-friendly method of calculating impact, as well as offering succinct, intuitive means of displaying the results (e.g. via biplots, Laverty et al. 2017a, and triplots, Dickey et al. 2018), we also propose that RIP could go some way towards closing the knowledge gap between scientists and managers/practitioners, readily informing prioritisation and control (Matzek et al. 2014).

Currently, successful implementation of RIP for real-world decision making is constrained by the lack of data on functional and numerical responses and their proxies. However, with university research laboratories and dedicated research facilities worldwide (e.g. CABI), and databases such as FoRAGE (Functional Responses from Around the Globe in all Ecosystems), there are growing opportunities to compile functional and numerical response data across a wide range of taxa, trophic levels and ecosystems (Dick et al. 2017a). This should lead to a readily accessible capacity to aid policy decisions and intervention. Once in place, RIP metrics offer considerable promise for aiding the management of invasive species and pests, and we call for their usage as a vital component of risk assessments and horizon scans, thus facilitating the assessment and prioritisation of invaders as required by EU legislation and global biodiversity targets.

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## Supplementary material 1

**Table S1. Outline of different numerical response proxies available, guidance for their use and the advantages and disadvantages of each**

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